

A NEW SPECIES OF FROG OF THE GENUS *ELEUTHERO-*
DACTYLUS (AMPHIBIA: LEPTODACTYLIDAE) FROM
THE COCKPIT COUNTRY OF JAMAICA

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Among the more prominent geological features of Jamaica are the extensive jagged limestone hills of the Cockpit Country. The harsh terrain of this area has long discouraged herpetological collecting, but recently two new species have been described from the more accessible periphery of the Cockpits (Schwartz, 1971; Thomas, 1975). Since similar karst areas on other Greater Antillean islands harbor endemic faunas, these discoveries indicated that the Cockpits might also. With this in mind, Jeremy F. Jacobs and I walked several miles overland into the southwestern Cockpits in the summer of 1974. The trip in was arduous and not particularly productive, but while walking out we collected two specimens of a distinctive small *Eleutherodactylus*. We returned to the area for two days and a night in July 1975 and collected several more specimens. We then walked the remaining distance across the Cockpits, from south to north, sampling as many different habitats as possible before emerging near Deeside.

Eleutherodactylus sisypodemus, new species

Fig. 1

Holotype.—National Museum of Natural History (USNM) 200000, a gravid female from the vicinity of "the cave" about 4 mi WNW Quick Step, Trelawny Parish, Jamaica, collected by Jeremy F. Jacobs and R. I. Crombie, 12 July 1975.

Paratypes (4).—Museum of Comparative Zoology (MCZ) 89138, same data as holotype; USNM 200001, same locality as holotype, collected by Barbara A. Harvey and Jeremy F. Jacobs, 12 July 1975; Albert Schwartz Field Series (ASFS) V28447, same locality as holotype, collected by R. I. Crombie, 12 July 1975; USNM 200002, on trail between "the cave" and the road north of Quick Step, Trelawny Parish, Jamaica, collected by J. F. Jacobs and R. I. Crombie, 29 August 1974.

Referred specimens (2).—USNM 200004, same data as holotype; USNM 200003, on trail between "the cave" and the road north of Quick Step, Trelawny Parish, Jamaica. Collected by J. F. Jacobs and R. I. Crombie, 29 August 1974 (cleared and stained).

Diagnosis.—A small species (males to 13.8, females to 17.9 mm snout-vent length) that is easily distinguished from all other Jamaican *Eleutherodactylus* by the presence of a calcar and denticulate tarsal finge, limited dorsal pattern polymorphism, and the black ventral coloration.



Fig. 1. *Eleutherodactylus sisymphodemus*, new species, holotype (USNM 200000); snout-vent length 17.9 mm.

Description of holotype.—A gravid female with the following measurements (mm): snout-vent length (SVL) 17.9; head length (HL) 7.1; head width (HW) 7.0; tympanum diameter (TYM) 1.5; eye diameter (EYE) 2.2; naris-eye distance (NE) 2.0; femur length (FEM) 8.2; tibia length (TIB) 8.1; foot length (FT) 8.2. Head slightly longer than broad; HW/SVL 39.1%. In lateral view, snout protruding; canthus rostralis rounded; loreal region slightly concave; lips not flared. Nostrils lateral, much closer to tip of snout than eye; diameter of eye slighter greater than distance from naris to eye; interorbital distance 2.7, greater than eye diameter. A single prominent tubercle in center of each eyelid with several more indistinct ones posteriorly and along edge of eyelid. Tympanum round, distinct, not sexually dimorphic in size. Tongue lanceolate but not nicked behind, free

for more than half its length posteriorly. Choanae small and round; pre-omerine dentigerous processes in two long, arched series extending from level of inner choanal border almost to palatal midline; separated by a distance equal to diameter of a choana. Fingers relatively short, unwebbed, with faint lateral fringe; III, IV, II, I in order of decreasing length. Digital pads flattened, longer than wide and distinctly pointed, with a circumferential groove. Several large, flat palmar tubercles; basal subarticular tubercle enlarged and flattened; a single additional subarticular tubercle present only on fingers III and IV; no supernumerary tubercles; a single pale ulnar tubercle on each arm. Toes long, unwebbed; IV, III, V, II, I in order of decreasing length; distal subarticular tubercles flattened and enlarged except conical and small on toes IV and V; several low conical plantar tubercles; a pale, swollen inner metatarsal tubercle. Digital pads similar to those on fingers but slightly larger. Heels not quite touching when femora at right angles to body axis; TIB/SVL 45.2%. A prominent, fleshy triangular spur at metatarsal-tarsal articulation and a larger one at tibio-tarsal articulation, joined by a scalloped dermal fringe; a less distinct fringe on both anterior and posterior faces of tibia. Anus directly posteriorly, with a series of four pale warts and an irregular black blotch just above it. Skin of dorsum smooth with two vague scapular warts and several irregularly scattered smaller pustules especially on upper surfaces of hindlimbs. A glandular lateral ridge continues from eye to about midway between limb insertions where it breaks up into a series of low tubercles. Venter smooth to finely shagreened, becoming slightly areolate near vent and bases of thighs.

Coloration of holotype.—In life the dorsal ground color was slate gray, slightly paler laterally, with a faint silver middorsal hairline. A wider golden stripe extended from tip of snout, through the nostril, across edge of upper eyelid, and onto the lateral ridge where it faded before reaching the groin. Below this stripe, the entire lateral surface of the head was black; this mask extended to and covered the tympanum, beyond which it narrowed to a sharp point near where the lateral ridge ended. The two scapular warts and the supra-anal tubercles were dirty white; there was a black smudge just above the row of supra-anal warts. Dorsal surfaces of the limbs were lighter gray, suffused with tan; thighs were banded with darker gray with irregular black patches at the knee. The forearm had a dorsal median black spot which extended onto the inner surface. A pale dot was present at the base of each digital pad, on both dorsal and ventral faces of digit.

The venter was charcoal gray to black with irregularly shaped silver flecks; the larger flecks were concentrated in the pectoral area and on the upper arms and thighs. Undersides of the limbs were slightly lighter gray; palms of the hands were black with a silver spot at the base of each

digit and undersides of the pads were gray. A wide black stripe covered the ventral surface of the lower arm, blending with the dorso-lateral spot. Posterior faces of the thighs were black, forming a triangular "seat patch" with its apex at the anus. The posterior edge of the tarsi and soles of the feet were also black; ventral sides of the pads and tarsal fringe were contrasting lighter gray. There were no "flash colors" but the inguinal areas were lighter gray. The iris was coppery red.

Morphological variation.—Four gravid females (including the holotype) have the following measurements (mm) and proportions: SVL 15.6–17.9 (\bar{x} = 16.9); HL 6.5–7.1 (6.8); HW 6.0–7.0 (6.6); TYM 1.3–1.6 (1.5); EYE 2.0–2.2 (2.0); NE 1.8–2.1 (2.0); FEM 7.2–8.2 (7.6); TIB 7.3–8.1 (7.6); FT 6.9–9.2 (7.5); TIB/SVL 44.0–46.8% (45.0); HW/SVL 38.5–40.0% (39.1).

The two adult males have the following measurements and proportions: SVL 12.0–13.8; HL 5.4–5.5; HW 4.8–5.6; TYM 1.3–1.7; EYE 1.6–1.8; NE 1.5–1.8; FEM 5.8–6.7; TIB 6.0–6.7; FT 5.5–6.4; TIB/SVL 48.6–50.0%; HW/SVL 40.0–40.6%. Both have vocal slits.

A single juvenile (USNM 200004) measures 7.9 mm SVL.

Morphological differences in the sample are slight. The angle of the prevomerine teeth series ranges from very slightly to distinctly arched; subarticular tubercles on hands and feet are variably flattened or conical, possibly due to differences in mode of preservation. The character showing greatest variation is texture of the dorsal skin.

Four specimens (MCZ 89138, ASFS V28447, USNM 200003, females; and USNM 200001, male) have prominent conical lumbar tubercles. Of these individuals, MCZ 89138 and USNM 200003 have additional distinct tubercles only at the scapula. USNM 200001 has paired, unpigmented scapular and sacral tubercles plus scattered obscure warts on the lateral areas. ASFS V28447 has extreme development in rugosity; both lumbar and scapular warts are well developed and they are joined by two almost complete rows of para-vertebral tubercles.

Other individuals (USNM 200000, 200002, and 200004) lack lumbar warts and have, at best, only vague additional dorsal ornamentation. However, the tarsal fringe is very distinct in all specimens, even the juvenile.

Myology and osteology.—In light of recent hypotheses on the polyphyletic nature of the genus *Eleutherodactylus*, one specimen (USNM 200003) of *E. sisypodemus* was dissected and later cleared and stained to determine the state of characters used by Heyer (1975:33) in his analysis. State terminology of Heyer is given in parentheses.

Jaw musculature: The depressor mandibulae consists of three distinct slips with origins on the fascia, squamosal, and annulus tympanicus (DFSQat, in the terminology of Starrett, 1968; State A of Heyer) with the annulus tympanicus slip being distinctly reduced. In the adductor

musculature of the squamosal, only the a.m. posterior sub-externus is present (State B).

Hyoid musculature: The geniohyoideus medialis is basically contiguous medially (State A), but with some very slight medial separation. The anterior petrohyoideus attaches on the lateral edge of the hyoid plate (State A). The sternohyoideus insertion is entirely near the lateral edge of the hyoid body (State A), but its attachment is very short and restricted to the region of the alary process. The omohyoideus inserts laterally on the posterolateral process of the hyoid (State I).

Thigh musculature: The iliacus externus is long, extending almost to the tip of the ilium. The tensor fasciae latae inserts on the anterior end of the ilium immediately anterior to the iliacus externus and the two muscles are contiguous for a considerable length (State F). Interior and exterior parts of the semitendinosus are approximately equal, displaced and attached by a tendon (State D). The adductor longus is absent (State D).

Cranial osteology: The quadratojugal is present and contacts the maxilla (State A); there is very slight contact between the nasals and frontoparietal (State A). The otic ramus of the squamosal is much longer than the zygomatic ramus, and approximately as long as the ventral ramus (State G). There is extensive median contact of the prevomers (State C) but no prootic/frontoparietal fusion (State A). The only exceptional element in the skull is the broad, rather heavily ossified lateral expansion of the otooccipital, creating a surprisingly solid posterior cranium for such a small frog.

Postcranial osteology: The posterior sternum has a partially mineralized mesosternum and a cartilaginous xiphisternum (State C; most similar to fig. 4-J in Heyer, 1975:18). The sacral diapophyses are rounded and the transverse processes of the presacral vertebrae are long and slender. The terminal phalanges are distinctly T-shaped and there are prominent humeral and ilial crests.

Pattern polymorphism.—Jamaican *Eleutherodactylus* are known to exhibit a bewildering variety of dorsal colors and patterns (Goin, 1954, 1960 and papers cited therein). *E. sisymphodemus* seems comparatively conservative in its variation. Since there are so few specimens involved, the pattern of each is discussed separately.

Holotype, USNM 200000: This specimen exhibits the simplest pattern type, an essentially unicolor dorsum with faint middorsal hairline and supra-anal dark splotch. Previously discussed.

USNM 200002, male: Similar to the holotype, with distinct hairline and small anal blotch but no other dorsal markings.

USNM 200001, male: Distinct hairline, but lumbar warts are surrounded by an irregular dark spot (pelvic spot of Goin, 1960:256, fig. 7). There is no dark anal patch and the legs are indistinctly barred.

USNM 200003, female: Similar to 200001 but with more distinct leg barring and a small anal patch.

MCZ 89138, female: Faint hairline, distinct dark lumbar spots and paired, smaller supra-anal spots. There is very faint suggestion of a dorsal "picket" pattern (Goin, 1960:250, fig. 3), but the "picket" is slightly darker than surrounding ground color. Legs distinctly barred.

ASFS V28447, female: Extremely faint hairline. A distinct dark "picket" outlined by tubercles. The lumbar spots are large and several outlining warts of the picket, including the scapular warts, are darkened.

USNM 200004, juvenile: No hairline. A large, pale, sub-rectangular mid-dorsal patch. The lumbar spots are white. One other specimen (an adult that was lost on the cross-Cockpit hike) exhibited this pattern.

Variation in color was slight. Dorsal ground color in life ranged from rich, milk chocolate brown (ASFS V28447) to the slate gray of the holotype.

Ventral color was uniformly shiny dark gray to black. The number of silver flecks was variable, but most individuals had more extensive, more evenly distributed flecking than the holotype.

The middorsal hairline (middorsal stripe of Goin, 1960:251, fig. 4) is common in West Indian *Eleutherodactylus*. Eleven of the 16 Jamaican species of the genus (8 of the 10 members of the *gossei* group) exhibit this morph (Goin, 1960; Schwartz and Fowler, 1973; Crombie, pers. obs.). It is a relatively consistent element of the pattern in all *E. sisypodemus*, except the "dorsal blotch" morph.

Of the three basic morphs in the sample, the picket pattern is relatively rare in *Eleutherodactylus*, it is found only in two members of the *gossei*-group (*gossei* and *pantoni*) and one mainland middle American species (Goin, 1960). The picket in *sisypodemus* differs from the typical pattern in that the picket is darker than the surrounding ground color rather than lighter as in the other species exhibiting the morph.

Goin (1960:256) reported without documentation that the pattern of bilaterally symmetrical "pelvic spots" (= lumbar spots) was "widespread in the genus." In Jamaican species the morph is restricted to members of the *gossei*-group. *E. andrewsi* almost invariably has this pattern, but individuals have been found with spots of differing size and shape, one spot, or no spots, although the latter is rare. *E. gossei*, *nubicola*, *pantoni*, and *luteolus* occasionally have some trace of lumbar spots and *E. fuscus* shows the morph more commonly (Schwarz and Fowler, 1973; Crombie, pers. obs.).

The pale "dorsal blotch" appears unique in Jamaican (and possibly all West Indian) *Eleutherodactylus*.

Comparisons.—*Eleutherodactylus sisypodemus* is the smallest Jamaican frog; this fact, coupled with the tarsal ornamentation will easily distinguish it from all other species. When the first specimens were collected, I noted their resemblance to *E. andrewsi*, a species restricted to moderate ele-

vations in the Blue Mountains, far to the east of the Cockpits. *E. andrewsi* frequently has a unicolorous dorsum with dark lumbar spots and a heavily pigmented venter. However, *E. andrewsi* is a highly vocal frog, and the ventral ground color is usually light with an extensive dark reticulum or spotting. The slightly larger size, occasional pale reddish flash colors, absence of limb fringes, and isolated distribution further distinguish that species.

E. sisyphodemus and *E. luteolus* are syntopic at the type-locality of the former. They are similarly sized, but adult *luteolus* usually have bright yellow bellies. Some *luteolus* juveniles are dark; one specimen (7.8 mm SVL) was originally mistaken for *sisyphodemus*. However, the lack of a black ulnar stripe and tarsal fringes distinguished it from the similarly sized (7.9 mm SVL) *sisyphodemus* juvenile; therefore, it is relatively easy to identify even recently hatched material.

The only other species with which *sisyphodemus* could be confused is *E. junori*. The loud, distinctive voice of *junori* was not heard in the deep Cockpits, but I have collected the species in the southeastern Cockpits, northwest of Troy. *E. junori* is a small species (19–27 mm) but with bright red flash marks in the groin and the characteristically variable dorsal pattern of most *gossei*-group members (see *Relationships*).

Relationships.—I divide Jamaican *Eleutherodactylus* into the following four groups, arranged in approximate order of decreasing SVL (I = introduced species).

<i>gossei</i> -group	<i>ricordi</i> -group	<i>auriculatus</i> -group	<i>jamaicensis</i> -group
<i>pantoni</i>	<i>cundalli</i>	<i>johnstonei</i> (I)	<i>jamaicensis</i>
<i>nubicola</i>	<i>cavernicola</i>		
<i>fuscus</i>	<i>grabhami</i>		
<i>gossei</i>	<i>planirostris</i> (I)		
<i>orcutti</i>			
<i>alticola</i>			
<i>andrewsi</i>			
<i>junori</i>			
<i>luteolus</i>			
<i>sisyphodemus</i>			

Schwartz (1969) characterized the *auriculatus*-group as moderate-sized frogs with a granular belly, short patchlike vomerine series, and well developed digital pads; most are vocal and call from arboreal sites. Schwartz (1969:114) hesitantly listed *E. jamaicensis* as a Jamaican representative of the *auriculatus* assemblage but noted that it was inconsistent in many ways with his concept of the group. I concur with this evaluation, but feel that the differences warrant exclusion from the *auriculatus*-group.

Schwartz (1958; 1969:102) attributed the following characters to the *ricordi*-group: rugose dorsum; long vomerine series; smooth or feebly rugose-venter; feeble digital pads or enlarged ones restricted to the two outer fingers; faint, insect-like call. The four species listed above fit well within this grouping; therefore, I do not recognize the "*cundalli* group" of Goin (1954:185).

Goin (1954:185) defined the *gossei*-group as follows: feebly developed digital pads; smooth back and belly; long vomerine series; red flash colors in the groin and on concealed portions of legs; vocal frogs with terrestrial calling sites. The group is somewhat more heterogeneous than Goin implied, but with the addition of two species my arrangement agrees with his.

Goin felt that absence of red flash colors in *E. luteolus* warranted its exclusion from the *gossei*-group, but *luteolus* occasionally has red or orange pigment in the groin and inguinal areas. In addition, Goin overlooked the fact that bright colors were variable in other species he included in the group (absent in *nubicola*, present or absent in *gossei* and *andrewsi*).

I tentatively follow Schwartz and Fowler (1973:126) in considering *E. orcutti* a specialized member of the *gossei* assemblage. This species has webbed feet, large digital pads, rugose dorsum, and no flash colors, all of which were interpreted as adaptations to a streamside niche.

E. sisymphodemus is similarly specialized for existence in a restricted habitat. The species resembles other *gossei*-group members with its squat body shape, short legs, and long vomerine series, but the tuberculate dorsum, moderately well developed digital pads, and tarsal fringe are rare or unknown in the group. Most of these characters are adaptive for the forest floor-leaf litter niche the species occupies. Pending further studies, I consider *E. sisymphodemus* a somewhat anomalous member of the *gossei*-group.

Natural history.—The steep ridges of the Cockpit Country are part of the "White Tertiary or Quaternary limestone formation" (Versey, 1972). These ridges are often greatly eroded from the effects of heavy rainfall (100–150 inches/year) and underground rivers; sinkholes and large soil-filled solution pockets are common and huge boulders or rock outcroppings litter the slopes. Footing is precarious since the limestone is brittle and breaks off in hand or underfoot. A thick layer of wet leaves further hinders walking and often conceals deep sinkholes or other natural pitfalls.

The vegetation of the Cockpits is "wet limestone forest" (Asprey and Robbins, 1953). The slopes are covered by a heavy growth of saplings interspersed with occasional larger hardwood trees (*Cedrela*, *Brosimum*, *Nectandra*); the canopy is complete and about 20–40 feet in height. The undergrowth is not thick and is primarily composed of climbing aroids, ferns, lianas and other epiphytes. Tank bromeliads are not especially

common in the understory but are more numerous high in the canopy or on exposed outcroppings.

The valleys or Cockpits between the ridges are normally thick with low vegetation and larger trees but most of the more accessible valleys have been cleared for cattle grazing and/or cultivation. In the distant Cockpits, care of crops is sporadic and heavy secondary growth of wild plantain, wild yam, thatch palm, and other feral plants is common.

About two miles north of Quick Step on the as yet unfinished cross-Cockpit highway is a small road leading to a lean-to, beyond which is a small agricultural area. An obscure path leads through a corn field, a small grove of citrus, and then into the shaded coolness of the Cockpit forest.

"The cave" is well known to residents of southern Trelawny, but it is infrequently visited because of local lore concerning the somewhat truculent spirits that inhabit the area. The cave is on the third ridge, about two miles by foot from the lean-to. The valley at the base of the cave ridge is badly overgrown and hasn't been grazed for several years; the ridge slopes gently at the bottom but becomes progressively steeper and more boulder-strewn as one nears the cave's mouth.

All of the specimens of *E. sisymphodemus* were taken in the heavy leaf litter on this or similar ridges. The first 1974 specimen was collected as it hopped across the trail on the second ridge; it apparently had been disturbed by the first people in the line. The second specimen was found on the opposite side of the same ridge in the litter of a bromeliad we had dismantled. We were unsure whether it had come from the bromeliad or had been aroused from the leaf litter by the activity. In 1975, all the specimens were taken on the cave slope. One female was found crossing the trail during the day as we first ascended towards the cave mouth. After dark we collected several more specimens (mostly lost later on the trek through the Cockpits) by shuffling through a pocket of leaf litter until a frog came out.

No call was heard that could be attributed to *E. sisymphodemus* but the choruses of other species were so intense that a quiet call could easily have been overlooked. *Eleutherodactylus pantoni* was the dominant voice in the nocturnal din, but the soft call of *E. luteolus* was also common. An irregular, high-pitched whistling tentatively traced to *E. grabhami* was unlike that recorded for the species elsewhere in its range. *E. gossei* was absent from the forest and only a few individuals were calling from the valley. A *cundalli*-like *Eleutherodactylus* was found in seepage areas of the cave and one large female was collected just outside the cave mouth on a leaf. Other anurans participating in the nocturnal chorus were: *Hyla wilderi*, *Osteopilus brunneus* and *Calyptahyla crucialis*; several unfamiliar calls were also heard.

No reproductive activity was noted in the field but all females collected contained large, unpigmented eggs; USNM 200003 contained six ova (0.5–1.0 mm diameter) in the left oviduct and three smaller ones in the right oviduct. The stomach contents of this individual contained the remains of ants and a winged hymenopteran.

The cryptic, leaflike body shape of *E. sisyphodemus* is reminiscent of several species of forest-floor dwelling leptodactylid and microhylid frogs. The cryptic coloration, absence of flash markings, and the tarsal decoration are obviously additional adaptations for life in the leaf litter community. Since this distinctive species remained undiscovered for so long, the possibility exists that it may be ecologically restricted to well shaded, undisturbed, wet limestone forest. This hypothesis was supported by considerable collecting in slightly disturbed parts of the Cockpits where leaf litter was present but subject to periodic drought due to the incomplete canopy of the disturbed forest. Intensive search in these areas yielded only *E. luteolus*, *pantoni*, and *grabhami*. I anticipate that *E. sisyphodemus* will be found throughout the Cockpits in suitable habitat and possibly also in other areas of wet limestone forest (e.g., Mt. Diablo on the border of the Parishes of St. Ann-St. Catherine). Several other species of wet forest frogs (*Hyla marianae*, *Eleutherodactylus grabhami* and possibly *E. junori*) have disjunct populations on this isolated limestone plateau.

Etymology.—The name is Greek, loosely derived from “demos,” district or country, and “Sisyphus,” a king of mythology whose tenure in Hell was spent endlessly rolling a large stone to the top of a hill only to have it roll back down again.

As we climbed the fiftieth of what seemed an unending series of steep, crumbling limestone ridges clothed in luxuriant vegetation and inhabited by opaque clouds of mosquitos, we began to gain an appreciation of all things Sisyphian. However, the experience gave us insights into the paradox of why Sisyphus was a happy man.

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My good friend Menocal Stephenson of Quick Step first introduced me to the Cockpits in 1970. Since then, his assistance and hospitality have been largely responsible for the success of my collecting in the Parishes of Trelawny and St. James. Lester Haggis, also of Quick Step, was a dependable guide and good company on the long walk across the Cockpits.

Albert Schwartz kindly examined the 1974 specimens at my request and confirmed the fact that they represented a new species.

George R. Zug, W. Ronald Heyer, and Frances I. McCullough (Smithsonian Institution) read and commented on the manuscript; Ron Heyer kindly examined the musculature of the new species in the course of his research, and Fran McCullough drew Fig. 1. I am grateful to all for their assistance.

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